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BIOLOGICAL BULLETIN.

ABNORMALITIES IN THE CESTODE MONIEZIA EXPANSA. II.

C. M. CHILD.

1. *Spiral Abnormalities.*

In the cases described in this section spiral modifications of the segmentation are present in greater or less degree. Associated with these are often found examples of partial division resembling those described in Part I, *Biological Bulletin*, Vol. I, No. 5. Where these are closely connected with the spirals they are shown in the figures and briefly described.

Figs. 24, 26, 27, 30, 38, 39, are selected from a number of different individuals. The other figures are all taken from the single worm mentioned in Part I as possessing a very large number of abnormalities. Figs. 34 and 35, being taken from a point nearer the anterior end of the chain, where the size is much less than in older proglottids, are magnified about fifty diameters, the other figures about twenty.

For terms used in the description, the structure of the normal segment, etc., the reader is referred to the first paper (*Biol. Bull.*, Vol. I, No. 5).

Figure 24.

The principal feature of this figure is a case of partial division, which is in reality a short spiral. The proglottid *a* shows at the right a very short furrow extending from the edge a short distance over the upper surface and ending free.

The lower surface shows no corresponding furrow. The length of the proglottid at this side is somewhat greater than, but not double, the normal length, *i.e.*, it is not as long as two fused proglottids of the same age. Two groups of cells, the "Anlagen," of the reproductive organs or "genital masses," appear upon this side, however, as would be the case if the short partial furrow were complete. The furrow itself indicates the imperfectly double character of the segment, and the two genital masses show this still more clearly. At the left *a* is only half as long as at the right and possesses only a single genital mass. The partial segment *b* is completely separated from *a* both on the upper and lower surface, but is seen to be connected with *c* on the lower surface. The furrow separating *b* from *a* runs inward and somewhat anteriorly from the left edge for about one-third the width of the body, then turns and extends outward and anteriorly until it joins the complete furrow in front. Thus the small piece *b* is completely marked off on the upper surface, and though its edge at the left side is of normal length, it narrows to a rounded end. On the lower surface the relations are different, for the partial furrow between *b* and *c* on this surface ends free, while the complete furrow separating *a* and *c* at the right bends so as to pass posteriorly to *b* at the left and connects at the left edge with the furrow between *a* and *b*. The partial segment *b* is thus a short spiral, making less than half a turn. Notwithstanding its small size, it shows a genital mass as large and distinct as any at this stage.

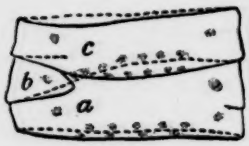

FIG. 24.

Figure 25.

Here two examples of partial division and a short spiral occur. Upon the upper surface the two partial proglottids *a* and *b* are incompletely separated, the partial furrow on the left side being longer than that on the right. The partial furrows at the right correspond exactly on the two surfaces, both ending free. The partial furrow on the upper surface at the left forms

the beginning of a spiral furrow which makes one and a half turns. It is oblique upon the lower side, running from between *a* and *b* at the left to the anterior edge of *b* at the right, then passing over the upper surface again as a complete transverse furrow anterior to *b*, and finally ending free on the lower surface. Thus the spiral segment *b* is open at both ends. If the furrow between *a* and *b* on the upper surface were complete, the spiral would begin between *a* and *b* at the right on the lower surface, and the furrow would thus make almost two turns. In the region where the genital masses appear the furrows show very nearly normal relations, and the position of the genital masses needs no comment.

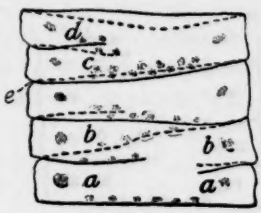

FIG. 25.

In *c d* another case of simple partial division occurs at the left, the partial furrow corresponding in position on the two surfaces. At the left two genital masses occur, while at the right, where *c d* is undivided and shorter than at the left, only one appears. All the partial furrows which extend far enough from the edges to lie within the region where the interproglottidal glands occur, possess them. The furrows between *a* and *b* on the right show none, as they are too short.

Figure 26.

This case consists of a short spiral in which the spiral furrow makes one and a half turns about the body. As the result of its course the partial proglottid *b* is formed, which unites on the upper surface with *a*, and on the lower with *c*.

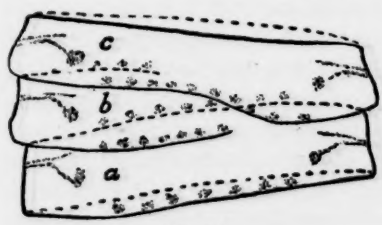

FIG. 26.

In the lateral regions the segmental boundaries are all normal, and, accordingly, the organs are situated nor-

mally, but at the left there are three segments and at the right only two, and a corresponding number of sets of genital organs is found.

Figure 27.

A spiral furrow making only a little more than half a turn appears in this case. At the left the upper surface of *a* is united at the edge with the lower surface of *b*, and at the right the lower surface of *a* unites at the edge with the upper surface of *b*.

FIG. 27.

The only abnormality visible at this stage in the genital organs appears at the left in *a*. Here the genital "Anlage" is elongated and narrower than in the other cases. The proglottid is not sufficiently developed to show the ducts and pores, so that it is impossible to determine just what the situation of these organs will be.

Figure 28.

Here the natural relation of the dorsal and ventral surface is somewhat altered. The figure is drawn with the dorsal surface uppermost, and it is seen that the furrows on the dorsal surface lie further posteriorly than those corresponding to them on the ventral surface. The furrows bounding *a* posteriorly do not meet at the edge, as they would if normal and merely distorted by pressure or otherwise, but the end of the ventral furrow is anterior to the dorsal. The furrows *d* and *d'* would correspond to each other if normal, but as a matter of fact *d'* meets *e* at the left edge instead of meeting with its corresponding furrow *d*, thus producing a slight spiral. The furrows *e* and *e'* would meet at the two edges if normal, but here again the ventral furrow is considerably anterior to the dorsal except at the right edge, and its left end shows no indication of bending posteriorly to meet the latter. A somewhat similar condition is seen frequently in mounted specimens, but in most cases is simply a distortion due to the compression between glass plates during fixation. The real abnormalities such as occur

here can be distinguished by the fact that at one edge or the other or both the corresponding furrows on the two surfaces do not meet. That some distortion has also occurred in this case is probable from the fact that in the regions immediately outside and posterior to that of the figure otherwise normal segments are oblique dorso-ventrally, as if the dorsal surface had moved posteriorly over the ventral, or the ventral anteriorly over the dorsal. The segment *b* is bounded by a furrow beginning at *d''* and forming a spiral of nearly two turns, ending free on the ventral surface (*e'*). The genital organs *b'*, on the left side of *b*, lie almost between the dorsal furrow *e* and the ventral *d'*, and it is the only genital mass on the left for the whole spiral. The ovary and vitellarium, being nearer the ventral surface, appear between the furrows *d'* and *e*, while the ducts lying nearer the dorsal surface bend posteriorly, and their terminal portions appear posterior to the furrow *e* on the dorsal surface, and finally reach the surface almost midway between the dorsal furrows bounding *b*. At first glance it appears that if the position of the genital organs is correlated with the form of the proglottid, the duct should open somewhere in the region *c* instead of passing posteriorly under the dorsal furrow *e*, as it does. As a matter of fact, however, its position is the only one possible in the spiral proglottid *b*. Since the spiral segment *b* lies somewhat obliquely, *i.e.*, with its ventral surface somewhat anterior to the dorsal, the position of the organs at *b'* between the dorsal furrow *e* and the ventral *d'* is only apparent. In reality they are in about the normal position in their segment *b*. The outer end of the ducts is rudimentary, consisting of a scarcely visible strand of cells, and there is no enlargement in the region of the pore. Moreover, the inner end of the vas deferens instead of running anteriorly to the ovary and vitellarium, as is usual, is posterior to them, as seen in the figure (*b'*). This position of the inner end of the vas deferens posterior to the ovary is peculiar and is probably due to the oblique position of the segment *b*.

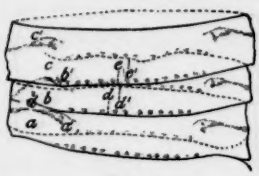

FIG. 28.

The rudimentary character of the terminal portion of the ducts is apparently due to the fact that the proglottid *b* is not wholly distinct from *a* in this region. The posterior dorsal furrow is interrupted at *d''*. The short portion extending to the left edge is not a furrow of normal depth but a scarcely visible fold upon the surface, and the left end of the main furrow at *d''* is also very shallow. On the ventral side there is no furrow corresponding exactly to the furrow *d'd''*, for *d'* is a spiral continuation of it. Therefore the only evidences of separation between *a* and *b* in this region are the slight furrows at *d''*. Since the degree of separation is so slight, the tendency to form a second genital pore and the terminal region of the ducts is probably very slight also, but is still present, as is evident from the figure. The testes are just beginning to appear (not represented in the figure), and their distribution corresponds exactly with the conditions on the dorsal surface.

Figure 29.

At the stage shown here the proliferating groups of cells forming the reproductive organs are visible, and the interproglottidal glands are more numerous. The variation is a spiral, the furrow making two complete turns. The posterior end of the spiral furrow appears between *a* and *b* at *c*. Upon the lower surface it is a complete furrow and is continuous with the furrow upon the upper surface between *b* and *d*. This bends anteriorly at the left instead of completing the furrow between *b* and *a*, and so separates *b* and *c* at the left edge, continuing over the lower surface as a complete furrow and passing once more to the upper surface between *d* and *c* at the right and finally ending free at *f*. The only portion of this continuous furrow which differs greatly in position from the normal is the part between *b* and *d* at the left on the upper surface, where it bends anteriorly and so fails to complete the separation between *a* and *b*. The spiral is the result of this bend

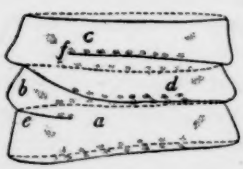

FIG. 29.

in the furrow, but since the furrow ends free at *e* and *f* both ends of the spiral proglottid bounded by it are open and connect respectively with *a* and *c*. The position of the genital masses is not affected by the presence of the spiral arrangement.

The general relation of the inter-proglottidal glands to the furrows is shown by the fact that the glands appear with the abnormal and partial furrows as well as with the normal.

Figure 30.

This figure shows two spirals situated in the regions designated by *a* and *b*. In each case the spiral is due to the curving of the furrow near the median line of the body. In the one case the curve is on the dorsal surface, in the other on the ventral. Since the curved furrows are on opposite surfaces and yet nearly parallel, the two spirals are opposite in direction. In both cases the ends of the spiral portions unite more or less completely with adjacent segments, owing to the fact that the furrows between them end free.

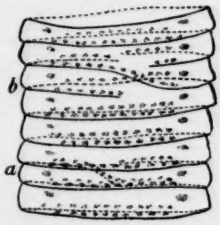

FIG. 30.

In *b* this union is much more complete than in *a*. In *a* the spiral furrow makes two turns about the body, in *b* only one and a half as a continuous furrow. If, however, the partial furrows at the right in *b* be considered as a continuation of it, this furrow also makes two complete turns.

The lateral regions and edges of the segments are all normal in form, and we find all the genital masses normal in position.

Figure 31.

The figure is a view from the dorsal side of a series of segments, showing a number of abnormalities. The first of these is the small partial segment *b*, wedged in at the right between *a* and *c*. Its dorsal surface is greater than its ventral, and its edge is nearly as long as that of a normal segment. Dorsally the furrow between *a* and *b* ends free on the surface. The

corresponding ventral furrow turns anteriorly a short distance from the edge and meets the main furrow between *a* and *c*. Thus the ventral surface of *b* is completely marked off from other segments. Both the dorsal and ventral furrows between *b* and *a* are rather shallow. The organs in *b* are distinctly abnormal. A rather small ovary and vitellarium appear nearer the edge than in normal segments, probably because of the increasing length of the segment *b* nearer the edge. The oviduct is incomplete and ends bluntly, as the figure indicates.

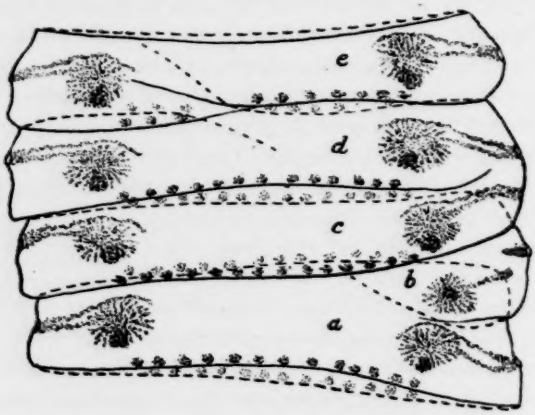

FIG. 31.

A distinct pore is present, and connected with it is a well-developed cirrus, but no trace of a vas deferens is found anywhere in the segment. The position of the various organs illustrates well the relation of each to the form of the segment in the region where it occurs. Thus the ovary and vitellarium, which appear from the dorsal surface to be near the posterior edge of the segment, lie midway between the bounding furrows on the ventral surface, and the oviduct, which extends somewhat dorsally from the ovary, runs obliquely forward towards the edge, so that it is normally placed with regard to the furrows on the dorsal surface. The pore lies near the anterior end of the segment. The ventral furrow bounding *b* anteriorly turns backward before reaching the edge and unites with the

posterior furrow, so that the region corresponding to the ventral side of *b* is cut into two parts, that nearest the edge being united with *c*, *i.e.*, taking *b* as it appears on the dorsal surface, we find that it is not separated from *c* at the edge. As *b* is bounded on the ventral surface it does not reach the edge of the body at all. The position of the pore is evidently connected with these peculiar relations. The dorsal side of *b*, together with *c*, forms a spiral. Beginning with the dorsal partial furrow between *b* and *a*, the spiral furrow makes two complete turns about the body.

The rudimentary condition of the organs in *b* is undoubtedly due to the small size of the segment. The ovary and the oviduct are more completely developed than the vas deferens. The segment *b* contains a number of testes and in some spermatozoa are visible.

The position of the organs in *a* needs no comment. The segment is of peculiar form, owing to the presence of *b*, but its genital organs are normally situated.

The furrows between *c* and *d* are abnormal. The dorsal furrow ends at the right without reaching the edge, and the ventral furrow turns posteriorly near the right edge and meets the posterior boundary of *c*. Thus the right edge of *c* and *d* is not divided by any furrow, but the dorsal furrow extends almost to the edge. The ovary and vitellarium at the right of *c* are normally placed with regard to the ventral boundaries, and the ducts and pore with regard to the dorsal boundaries. Both ducts cross the course of the ventral furrow at an angle to reach the edge, thus indicating that relations on the ventral side have little influence on their direction. At the right of *d* a normal set of organs occurs. The figure shows, however, that the two pores on the right edge of *c d* are near together. In the region of the inner ends of the ducts the segments are completely separated, and the distance between the two sets of ducts is normal here. As they approach the surface, however, the separation between the two segments on the dorsal surface becomes less and less complete, and the edge itself is undivided. Thus the pores tend to form near its middle, but the fact that the dorsal furrow extends so nearly to the edge

indicates that a certain degree of individuality exists up to and perhaps beyond the point where it terminates, and this, together with the length of the edge of *c d*, accounts for the presence of two pores instead of the union of both sets of ducts in a single pore.

Between the segments *d* and *e* the furrows are very abnormal. The ventral furrow is divided into two parts which overlap on the surface, the one turning anteriorly, the other posteriorly. The oblique portions are very shallow and do not bear interproglottidal glands.

The dorsal furrow is also in two parts. The one at the left does not turn posteriorly, but continues as a very shallow furrow over the region corresponding to that which the ventral furrows leave undivided, and finally unites with the right half. This latter, however, continues to the left, beyond this point, but turns anteriorly, running up into the segment and ending just dorsal to the ovary. The oblique portion is shallow, like the oblique portions of the ventral furrow, and bears no glands. The genital organs at the left of *d* and *e* are normal, however, doubtless because the growth has been normal in the regions where the organs occur. Only the oblique portion of the dorsal furrow approaches the ovary, but, as has been repeatedly shown, the position of the ovary is influenced only very slightly, if at all, by the form of the dorsal surface.

Figure 32.

At the stage of development shown in the figure the genital masses are becoming differentiated into the various organs. The female portion is mostly distinct from the male, and the strands of cells forming the ducts extend nearly or quite to the edge of the body, though the pores are not distinct as yet. The variation shown is a spiral in which the furrow makes two complete turns, the spiral segment bounded by it making one complete turn. The spiral begins on the right in the short furrow bounding *a* posteriorly and separating it completely from the proglottid behind; from this point it passes around the body, bending forward at the right side of the upper sur-

face to form the anterior boundary of *a*, then making one more complete turn and ending on the upper surface, thus leaving *b* and *c* incompletely separated at the right of the dorsal surface. The development of the genital organs is sufficiently advanced in this case to show the very intimate relation of these organs as regards position with the form and relations of the proglottids. The segment *a* possesses its own genital mass (*a'*), which is entirely separated from all the others. This is, however, of less than the normal size and does not reach the edge of the segment. It is divided into two parts in its inner portion, but the group of cells which would later form the ovary and vitellarium does not appear. In fact, the mass seems to consist largely, if not wholly, of portions of the two ducts. It will be remembered that the ducts lie farther dorsally than do the ovary and vitellarium. The figure is drawn with the dorsal surface uppermost, and it is only dorsally that the region *a* appears as a distinct partial proglottid. On the ventral surface the relations of the furrows are entirely different. It appears then that the dorsal region of *a* possesses a degree of individuality sufficient to cause the appearance of the organs proper to this region. The ventral region not being separated from *b*, the organs of the ventral side do not appear. Whether the organs would in later stages approach or reach the normal development it is impossible to state with certainty, but the evidence seems to be against such a view, for in all cases of similar abnormalities in much later stages the genital organs or parts, however rudimentary they may be, show the same degree of differentiation as those of normal segments.

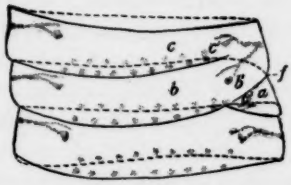

FIG. 32.

In the large, incompletely separated segments *b* and *c*, there appears another example of the close relation between the individuality of the segment and the presence and arrangement of the reproductive organs. At the left appear normal sets of organs in normal position. At the right, however, where the furrow on the dorsal surface is incomplete and that upon the

ventral surface bends posteriorly, two sets of organs (b' and c') appear whose ducts open into a common genital pore. Each of the sets is apparently complete, possessing the groups of cells which will form ovary and vitellarium, as well as the vas deferens. The inner portions of these two sets are situated much as they would be if b and c were normally separated from each other, *i.e.*, their position is nearly normal. The partial furrow on the dorsal surface, however, does not extend to the right edge of the body, but ends free before reaching it, so that b and c are united here, and correspondingly only one genital pore appears at d, and into this both sets of ducts open. But the question now arises as to the reason for the connection of the organs b' with this pore. Normally these organs would open on the edge at some point not far from f, but, owing to the arrangement of the proglottids in this case, f is the point of intersection of the furrows, *i.e.*, does not possess the features of the region where the genital pore normally appears, for this is upon the edge, about midway between two furrows. The only possible conclusion from the facts is that the direction of the ducts and their final connection with the pore are correlated with the form of the proglottids in this region and especially upon the dorsal side. This conclusion is confirmed by the fact that the ducts cross almost at right angles a furrow on the ventral side, thus rendering it evident that their arrangement is not affected by its presence. In short, ovaries and vitellaria arise separately in b' and c', because the relations of the ventral sides of the segments in that region are practically those which exist in two separate proglottids, and upon the dorsal surface the same is true in the immediate region of the inner portions of the organs. Nearer the edge, however, the relations on the dorsal side are those of a single segment, so that the two sets of organs approach each other and finally open in a common pore, which occupies a normal position with respect to the boundaries of the proglottid in its immediate vicinity.

Figure 33.

This figure shows a rather long spiral, together with a small completely separated partial proglottid. The furrows bounding the spiral begin between the partially separated segments *a* and *b* near the left side of the dorsal surface — the dorsal surface is uppermost in the figure — and make a little over three turns about the body. At the left side of the dorsal surface, between the segments *d* and *e*, the furrow becomes shallower, and on the left edge it terminates. The spiral segment enclosed by it makes a little more than two complete turns. In consequence of the course of the furrow, *a* and *b* are incompletely separated on the dorsal surface, but completely separated ventrally; the furrows bounding the regions *b*, *c*, and *d* do not correspond on the two surfaces, and finally *d* and *e*, which are distinct dorsally, are completely united on the ventral surface. These abnormal relations are accompanied by a number of corresponding abnormalities in the genital organs. At the left side *a* is distinct from *b*, and the genital organs *a'* on this side are normal and in normal position. At the left side of *b*, *c*, and *d*, where the spiral character of these segments becomes evident, the genital organs show marked abnormalities. At *b'* only two small groups of cells are found, representing apparently portions of the ducts; at *c'* and *d'* full sets of organs occur, but lie obliquely, and the ducts are elongated. It is evident that the pores and the greater portions of the ducts are normal in position with regard to the dorsal form relations of the segments. The oblique direction of the ducts is apparently due to the fact that the dorsal side of *c* and *d* bends forward near the left edge. Since the inner portions of the organs are formed at the normal distance from the edge, in order to reach the edge as they do, the ducts must be longer than the normal, for they must run obliquely.

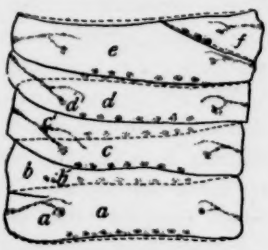

FIG. 33.

The dorsal sides of *b* and *c* both correspond in part, as

regards position, to the ventral side of *b*. The ovary of the set *c'* lies in *b* as bounded ventrally. Apparently the dorsal side of *c* and the ventral side of *b* are to be regarded as belonging together at the left, even though they do not occupy corresponding positions, as they do at the right. If this be the case, the organs *c'* show a close correspondence to the form relations. Upon the dorsal surface *b* is merely a small portion, intercalated, as it were, between *a* and *c* and incompletely separated from *a*. The genital organs are very rudimentary. The ventral organs found in *b* belong to the set *c'*, and there is no distinct ventral region corresponding to the dorsal side of *b*. Thus no ventral organs appear. Two small groups of cells (*b'*) are the only traces of genital organs in this region. These apparently represent portions of the ducts. This very slight development of genital organs is probably due to the small size and imperfect form of this portion.

The set of organs at *d'* shows much the same relations as that at *c'*. Its pore, however, is very close to the furrow between *d* and *e*, as is also the pore of the organs at the left of *e*, which are otherwise normal. The approximation of these pores is evidently correlated with the incomplete separation of *d* and *e* by a shallow furrow on the dorsal surface, and not at all ventrally.

On the right, at *f*, a small partial segment is separated from *e* by oblique furrows. It possesses a normal set of genital organs. The intercalation of *f* leaves the right edge of *e* very short, but the genital organs are, so far as appears, normal. Whether they will reach full development and normal size cannot of course be determined.

Figure 34.

The abnormalities figured here occur not far behind the scolex, where genital organs have not yet appeared. At *a* there is a small partial segment wedged in between two others at the left side. Just anterior to this is a spiral, beginning on the lower surface and making nearly two turns. The course of the spiral furrow is such that on the upper surface the segment *c* does not reach the left edge at

FIG. 34.

all, and on the lower surface the segment next to *a* narrows toward the left and ends at the edge.

Figure 35.

The figure shows a complex case of partial division (*a*) and a spiral of about four turns (*b c*). The region *a* is partially separated into two segments at the right, but at the left into three, the most anterior (*b*) forming the beginning of the spiral. On the lower side, just beneath *b*, there is a small region wholly marked off by furrows and not forming part of the spiral. The spiral *b c* is perfectly simple in form, though rather long. This case, like Fig. 34, was found near the anterior end of the chain, and neither genital organs nor inter-proglottidal glands are formed.

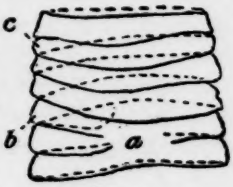

FIG. 35.

Figure 36.

The figure is a dorsal view of an extremely long spiral, which makes seven complete turns about the body. The spiral is due to the bending posteriorly of the ventral furrows near the right edge.

At the left the segments are all normal in form, and all of the genital organs are normally placed. At the right the curve in the ventral furrows produces complex relations in the various segments. All of the curved portions of the ventral furrows except the one anterior to *c* are much shallower than the transverse parts, as is indicated in the figure. In the one exception, the furrow anterior to *c*, the curved portion appears as distinct and deep as the rest of the furrow. In *a*, *b*, *d*, *e*, and *f* the inner portions of the organs of the right side are seen to lie in about their normal positions with respect to the boundaries of their segments. The ducts are parallel to the dorsal furrows and cross the course of the ventral furrows in each case, *i.e.*, they conform to the relations on the dorsal side. In the segment *c*, however, the ducts run nearly parallel to the

ventral furrows, crossing the dorsal furrow which forms the posterior boundary of *c*, and finally opening, together with the organs in *b*, into a single pore on the edge of *b*. This case appears to be an exception to the general rule of correlation between the arrangement of the genital organs and the form of the segment, for the ducts on the dorsal side cross the

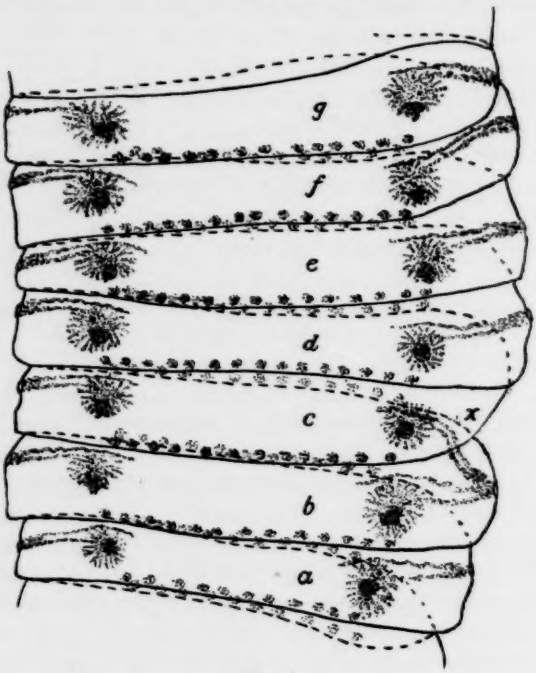

FIG. 36.

course of the dorsal furrow. As is evident from the figure, the ventral side of *c* and the dorsal side of *b* are very intimately connected at the right edge, more so than, for instance, the ventral side of *e* with the dorsal side of *d*. Moreover, the edge of *c* itself is oblique and very short, and the ventral furrow at *x* is deeper than the corresponding portions of the other ventral furrows. The course of the ducts from the organs at the right of *c*, differing as it does from the course of

the ducts in the other segments of the spiral, is undoubtedly determined by the relations existing here. Probably the small size of the dorsal side of *c* at the right is the real basis of the difference, for it is largely because of this that the ventral side of *c* is so intimately connected with *b* at the right.

The segment *g* is nearly normal in form in the region of the right ovary, and this lies in its normal position. Nearer the edge, however, the dorsal and ventral sides of the segment do not correspond, the ventral surface bending posteriorly, while the dorsal bends slightly in the opposite direction. The ducts and the pore evidently conform to the relations on the dorsal side, but they lie almost directly over one of the ventral furrows.

Figure 37.

This case comprises a number of segments which show an approach to the spiral form but do not quite attain it, since most of the furrows are not complete at the left. The figure is a dorsal view. It can easily be seen from the figure that if the furrows on the two surfaces were continued over the left edge, a spiral segment extending through the whole series would be formed. The manner in which a spiral arises is well illustrated by this case. The bending of the furrows near the edge on one surface is all that is necessary. Here the dorsal furrows bend anteriorly, while the ventral furrows remain straight, except between *a* and *b*, where there is a slight posterior curvature.

At the right the segments are all normally bounded, and the genital organs of the right side are normal in form and position. At the left, however, where the relations approach the spiral form, the organs show corresponding abnormal relations. At the left of *a* the anterior ventral furrow is normal in the ovarian region, but turns posteriorly near the edge, and the dorsal furrows bend anteriorly, so that the dorsal side of the segment appears curved forward at the left end. The ducts and pore show clearly the influence of this form. The course of the ducts toward the edge is oblique, *i.e.*, nearly parallel to the dorsal furrows in this region, and the pore lies nearly

in the middle of the edge as it is bounded dorsally. In *b* very similar conditions exist, but the bend in the dorsal surface of the segment is more pronounced than in *a*. The ducts are more oblique than in *a* and elongated, but preserve the same relations to the segment. The dorsal furrow forming the anterior boundary of *b* curves to such a degree that it does not reach the edge at all, thus leaving it apparently undivided, *i.e.*, not distinct from the edge of *c*. Near the middle of this common edge a single pore appears, and into this open the

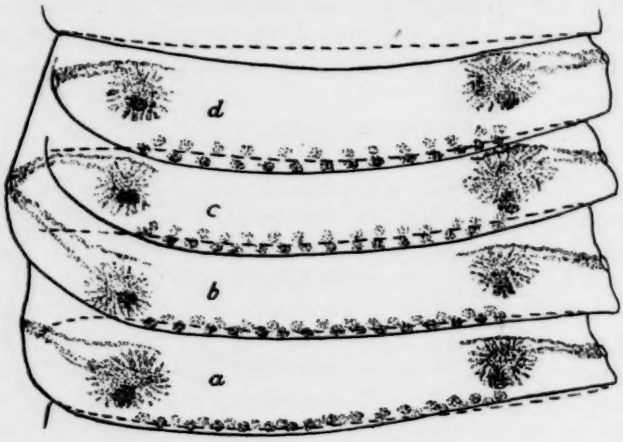

FIG. 37.

ducts from *c* as well as those from *b*. The ducts of the organs in *c* cross the course of the curved dorsal furrow to reach the edge, but this part of the furrow is very slight.

The organs at the left of *d* present an extremely interesting relation with respect to the furrow. The dorsal furrow between *c* and *d* turns anteriorly and runs parallel to the edge, but the furrow in front of *d* is straight. The ducts of the genital organs show no tendency to run parallel to the curved furrow, but meet it almost at right angles, and the pore appears in this furrow instead of upon the edge of the body. The furrow is deeper than the one posterior to it which crosses the ducts in *c*, apparently without affecting their position.

The difference in the relations in these two cases is undoubtedly due to the difference in depth of the two furrows. In the case of *d* the furrow is deep enough either to interrupt the course of the ducts or else to produce conditions approaching those at the edge of the body, and consequently the pore forms here instead of at the edge. The ducts are slightly shorter than the normal, but the inner portions of the organs show a perfectly normal arrangement.

2. *Other Abnormalities.*

Under this head are included a few cases of abnormalities of a different nature from those previously described. Two of these (Figs. 38 and 39) are cases of lateral duplication of the genital organs, and the other two (Figs. 40 and 41) are cases of alteration in position of the genital organs.

Figure 38.

The figure, a view from the ventral side, shows a number of abnormalities. Between the segments *a* and *b* the furrows are normal except near the right edge, where both curve posteriorly. On the ventral surface the furrow ends before reaching the edge, while dorsally it continues to the edge. The inner portions of the genital organs are normal, and the ducts extend in the normal direction toward the edge, but do not reach it. The pore lies on the curved dorsal furrow a short distance from the edge of the body, *i.e.*, on the dorsal surface. The terminal portions of the ducts are entirely normal in structure. Thus the abnormal edge formed by the curved furrow affords conditions which allow a normal pore and terminal organs to appear and so resembles closely the segment *d* in Fig. 37, except that there the furrow between *c* and *d* turns anteriorly instead of posteriorly. At the left of *a* the form of the segment and the organs are normal.

The segments *b* and *c* are incompletely separated on the ventral surface, and *c* is a spiral in consequence of the peculiar curve of the ventral furrow separating the parts *c* and *d*. On

the dorsal surface the furrows are normal, and the regions corresponding to *c* and *d* are parts of a single segment. Thus the spiral furrow bounding *c* and *d* begins ventrally between *b* and *c*, makes one turn, then bends anteriorly, separating *c* and *d*, next makes another almost complete turn and finally ends on the ventral surface anterior to *d*, so that *d* is not completely separated from the segment next anterior to it.

At the right of *b* the edge is very long in consequence of the curve in the posterior furrows, but there are indications that these curved portions of the furrows do not mark the

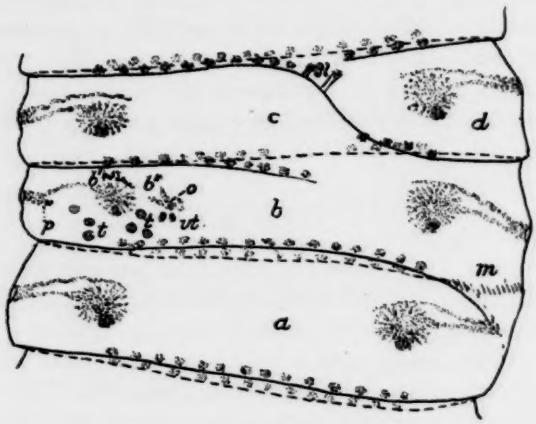

FIG. 38.

actual posterior boundary of *b*. Along the line *m* the cellular structure appears denser and stains more deeply, thus resembling in appearance the regions near the intersegmental furrows. There is no real furrow here, but the presence of this band of tissue similar to that which occurs along segmental boundaries indicates that the posterior boundary of *b* is here and not along the curved furrows; that is, these latter are mere wrinkles in the surface continuous with the intersegmental furrows. If this be the correct interpretation of the conditions here, it is evident that the ovary and pore at the right of *b* present the usual correlation in position with the form of the segment.

At the left of *b* peculiar conditions appear. Besides the organs (*b'*) in the normal position there is another partial set (*b''*) lying to the right of the first. The first set, although normally placed, is imperfect, for the ovary and vitellarium are rather smaller and less branched than usual; the oviduct, atrium, and pore are normal, but the vas deferens is not complete. Its inner end appears anterior to the ovary — near the letter *b'* — but it ends blindly posterior to the oviduct instead of in its normal position anterior to it. A peculiar condition appears in five or six of the testes (*t t*) near the edge. They are enlarged and packed full of spermatozoa, so that they stain like the vas deferens of this stage and are quite different in appearance from the other testes, though the testis cells can be distinguished in them with high powers. The inner portion of the vas deferens is also full of spermatozoa, but the seminal receptacle is empty, indicating that there is no outlet for the sperm into the female organs. In the normal organs of adjacent segments impregnation has already occurred. The accumulation of sperm in the testes (*t t*) is doubtless due to the imperfect development of the male ducts. The movement of the spermatozoa from the middle regions of the segment toward the edges having occurred as far as possible — the testes in the middle region are empty of sperm — they have accumulated in a number of testes near the edge and remain there, since there is no outlet to the exterior or to the female organs. This condition is found in one other case (Fig. 39).

The small size and imperfect development of the set of organs *b'* is probably due to the fact that the left half of the segment *b* is considerably shorter than the normal. The normal length at this age is about that of *a*, and this portion of *b* is only a little more than half as wide as *a*. At the right *b* is wider and normal organs occur.

The second set of organs (*b''*) is very small and rudimentary, consisting of a small simple ovary (*o*) and two small groups of cells representing the vitellarium (*vt*) without any traces of ducts. The orientation of these organs in the proglottid is apparently normal.

This transverse duplication of the female organs does not

appear to be connected with any visible abnormalities in the form of the segment or in the relations of its boundaries. The two sets of organs taken together probably do not represent more material than a single set of normal size. The left side of the segment *b* is somewhat shorter than normal, but in Fig. 39, *c*, where a similar duplication occurs, the segment is of very nearly normal length. The furrows bounding this region of the segment seem to be normal, except that the distribution of the inter-proglottidal glands in the dorsal furrow between *b* and *c* is rather irregular. None appear in this furrow in the middle region of the body, and only a few to the left of the middle. The furrow is normal in appearance, however, and the other furrows seem to be normal in every respect. The conditions found here may perhaps be due to the splitting of a single genital mass in earlier stages, but if this is the case no clue is afforded as to the cause of the splitting. If such a division should occur, later growth would undoubtedly increase the distance between the two portions. From a study of the early stages of the genital organs and their method of origin I am inclined, however, to believe that this extra set has arisen *in situ* and without connection with the set *b'*. If this is the case its appearance must be the result of certain internal conditions, which present no other visible manifestation.

This transverse duplication of organs constitutes a problem entirely different from that of their multiplication longitudinally. Whether or not it is to be regarded as the result of a kind of longitudinal division of the segment is doubtful. No organs except the ovary and vitellarium are duplicated in this case, *i.e.*, the organs on the ventral side only. This is likewise the case in Fig. 39. These two examples are the only ones of this nature which I have found so far, but it is hoped that additional material bearing upon this point may be discovered and may serve to throw some light on the factors concerned in the production of this peculiar abnormality.

The regions *c* and *d* of the ventral side are separated by a portion of the spiral furrow which runs almost longitudinally. At the right it forms the posterior boundary of *d*, but turns anteriorly and then continues as the anterior boundary of *c* at

the left. On the dorsal surface the furrows appear normal. Relations at the two edges are apparently normal, and the genital organs appear normal in all respects.

The relations of the inter-proglottidal glands to the abnormal furrows are interesting. Those portions of the furrow which run transversely show the glands in their usual position, but there are none in the region where the furrow departs from its transverse course. Two of the glands (*gl*) in the partial segment *d* present very peculiar relations to the furrow. Here the furrow bends posteriorly, but the last two glands appear at some little distance anterior to it and almost in line with the others and are connected with the furrow by distinct ducts of considerable length. In the posterior region of the curve two of the glands lie posterior to the furrow as it curves forward, but these open directly. The relation of the glands to this curved furrow affords further evidence in favor of the conclusion that the curved furrows do not always coincide with segmental boundaries. Here the glands do not follow the furrow in this curve, but lie at some distance from it and are entirely absent from that portion which departs farthest from the normal condition. It appears as if the glands follow the line of the real boundary, while the furrow does not. Nevertheless, as the presence of the ducts indicates, the glands tend to open in the furrow.

Figure 39.

The series of abnormalities occurring in the three segments represented here is in some respects the most peculiar that I have found in this species. The figure is a ventral view.

In the segment *a* the relations on the right are normal, but on the left there appears on the dorsal surface the anterior end of a spiral, the remainder of which is not drawn, as it makes only one turn and is similar to others already discussed. The ducts of the organs *a'* extend to the surface in accordance with the relations on the dorsal surface and thus open at a point on the edge which is dorsally a part of *a*, but ventrally in another proglottid.

The segment *b* is abnormally short, even more so dorsally than on the ventral surface. In accordance with this fact only partial organs are developed right and left (*lb'* and *rb'*). Ducts connecting with the surface do not appear at all, and on the left no pore is formed. On the right edge, however, a pore appears, of normal size and with atrium and a small portion of the oviduct extending inward from it. This portion was found upon examination to present the characteristic appearance of the oviduct and to possess a lumen, but was

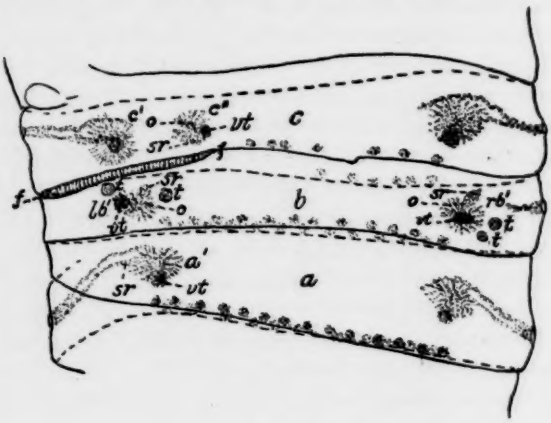

FIG. 39.

closed at the inner end. The reason for the appearance of a pore on the right edge and not on the left lies, I believe, in the fact that the right edge is longer than the left and thus presents more nearly the conditions of the normal edge. Each of the partial female organs *lb'* and *rb'* consists of a small ovary (*o*), a small vitellarium (*vt*), and the inner portion of the duct, terminating in a small, bladder-like, closed seminal receptacle (*sr*), which is empty. The organs of the dorsal surface are less nearly normal than those of the ventral. Testes appear, but their number is much less than the normal, even in proportion to the small size of the proglottid, for they are scattered very sparsely through the middle region, while other segments of this stage show large numbers of them. No traces of vasa

deferentia appear on either side. This rudimentary condition of the male organs is doubtless due to the extreme shortness of the proglottid. As on the left side of *b* in Fig. 38 the spermatozoa have accumulated in some of the testes in the lateral regions of the segment (*t t*). In this case there is no exit on either side of the spermatozoa, and the female ducts are incomplete and unconnected with the male ducts. Consequently the segment is not functional. The spermatozoa cannot fertilize the eggs of this or any other segment, and the eggs cannot be fertilized by spermatozoa from this segment or from any other.

The ventral furrow between *b* and *c* is distinctly abnormal, especially at the left. A normal furrow does not cut into the body vertically, but obliquely, and in such a manner that the posterior edge of each proglottid seems to overlap the anterior edge of the next succeeding. Over about two-thirds of its course the ventral furrow between *b* and *c* is normal in its relations, though slightly irregular in its course. Over the remaining third, however, — the shaded portion at the left marked *f*, — it is a vertical furrow widely open to the surface, and nearly twice as deep as the normal furrow by actual measurement. It cuts almost halfway through the body and thus separates *b* and *c* in this region much more completely than they are separated elsewhere. This portion of the furrow shows no inter-proglottidal glands, but they are present in the more nearly normal portion. The ventral furrow anterior to *c* is also abnormal at its left end. It is interrupted, one portion turning anteriorly, and the other curving near the edge so as nearly to enclose a small area. The dorsal furrow bounding *c* is normal.

In the segment *c* there are two normal sets of organs, the one situated normally, and the other nearly so ; but in addition to these organs a third set (*c''*) appears situated to the right of *c'* and consisting of a small ovary (*o*), a vitellarium (*vt*), and a small, empty seminal receptacle, which is closed. This case of transverse duplication of organs is very similar to the one figured in *b* in Fig. 38, and it is in the same region of the body, the two being separated by some thirty segments only. This second case does not afford any evidence as to the factors concerned

in the production of this form of variation. However, the position of the organs in *b* and *c* does bring to light some interesting facts regarding the orientation of the organs in the segment, indicating that this also is perhaps correlated with the "form" of the segment.

In the normal form of the female organs the vitellarium lies more or less completely posterior to the ovary, as is clear from many of the figures (see a' in segment *a* of this figure, for instance). The seminal receptacle appears at a point separated from the vitellarium by one-quarter of the circumference of the ovary, *i.e.*, about ninety degrees (note the position of *vt* and *sr* in a', where they are normally situated). Now in the supplementary set of organs c'', in the segment *c* the vitellarium lies on the right side of the ovary, while the small rudimentary seminal receptacle (*sr*) is posterior. That is, the whole set of organs appears as if rotated through an angle of ninety degrees from its normal position. An oviduct, if present and normally oriented with respect to the ovary, etc., would lead to the shaded portion of the furrow *f*.

Turning now to the organs lb' at the left side of *b*, we find that the parts present in this set are the same as those found in c'', *viz.*, a small ovary (*o*), a vitellarium (*vt*), and a small closed seminal receptacle (*sr*). The orientation of this group, however, is different from that of c''. The vitellarium, instead of being in its normal position posterior to the ovary, lies at the left of it, while the small seminal receptacle (*sr*) is anterior to the ovary, instead of to the left. Here, then, the whole complex appears as if rotated through an angle of ninety degrees in the direction opposite to that in which the rotation of c'' is conceived as having occurred. In consequence of this position, an oviduct, if present and oriented normally with respect to the other organs, would, as in the case of c'', open into the shaded portion of the furrow *f*.

Examination of the organs rb' at the right of the segment *b* shows that the relations there are more nearly normal. The vitellarium (*vt*) is somewhat posterior to the ovary, and the seminal receptacle, *sr*, though somewhat more than ninety degrees from the vitellarium, does extend in a nearly normal

direction, and if growth of the parts continued, the receptacle and the oviduct from the pore would meet. In brief, this set of organs shows what is practically the normal orientation, while *lb'* and *c''* do not.

The suggestion which offers itself in this connection is that the abnormal orientation of the organs *c''* and *lb'* is correlated with the presence of the furrow which lies between them. The furrow is on the ventral side, as are these organs. May it not be possible that the orientation of these two sets of organs with respect to this furrow is due to its extreme depth? They are oriented with regard to it as if it were the edge of the body, though no pores appear, opening into it. There is a considerable extent of free surface in the dorso-ventral plane on the sides of the furrow. The organs at *c''* are far from the real edge, but near this abnormal furrow, and their abnormal orientation appears to be a form of adaptation to the abnormal conditions. The complex of organs *lb'*, as described, is correspondingly oriented with regard to the furrow *f*. The question at once arises as to why this should be, since this set lies at the normal distance from the real edge. The answer to this question may lie in the fact that the left edge of the segment *b* and the region near it are very short — apparently too short to allow a pore and ducts to appear. The organs at *lb'* are much nearer to the furrow *f* than to the edge, and if the orientation of *c''* is determined by the furrow, that of *lb'* may be also. In the organs *c'* orientation and position are apparently normal. The pore lies rather far anteriorly, and this is probably due to the fact that *c* is incompletely separated dorsally from the segment next in front. The position and orientation of this set of organs may seem to be strong evidence against the conclusion that the orientation of *c''* and *lb'* is due to the presence of the furrow *f*; but here the edge is normal and the proglottid is of normal length, *i.e.*, normal relations are possible here, while they are not in the cases of *lb'* and *c''*. Furthermore, on the right of *b*, where the furrows are both normal, and the edge is wider than at the left, the organs are normally oriented and a pore is present, though the parts are not connected.

All who study the cases discussed in this and the preceding paper must, I believe, conclude that the position and arrangement of the genital organs in abnormal as well as in normal proglottids are very definitely determined by the form relations

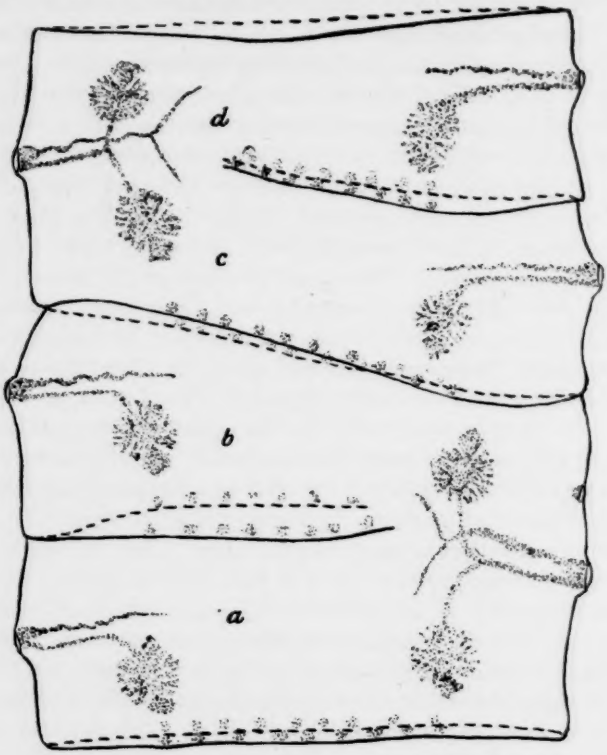

FIG. 40.

of their segment. The above suggestions have been made in the belief that the form relations may have some influence here, and in the hope of throwing some little light on the conditions in this particular case. Whether other similar cases, if found, will confirm them remains to be seen.

Figure 40.

Two cases of partial division are figured here as seen from the dorsal surface. The two are almost exactly similar, except that in one case the partial furrows extend from the left edge, in the other from the right. At the side of the body, which is completely divided in each case, two complete sets of genital organs normally situated are found. At the other side the inner portions are double, but the ducts unite to form a single

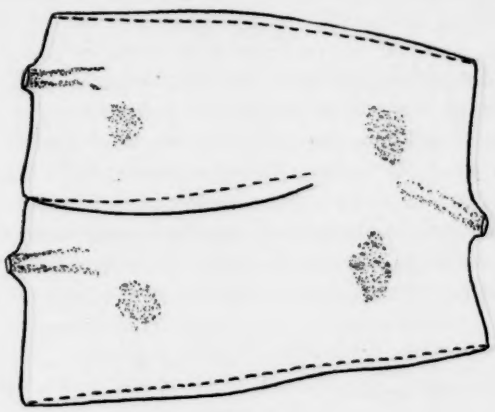

FIG. 41.

vas deferens and a single oviduct, and these open through a single pore, which is situated almost exactly in the middle of the undivided edge. The most remarkable fact is that the position of the anterior set is the reverse of that of the posterior set in each case, the oviduct running posteriorly from the ovary, and the vitellarium lying anterior instead of posterior to the ovary. The vas deferens also runs posteriorly instead of laterally. The arrangement of the organs is very evidently correlated with the incomplete separation of *a* and *b* and of *c* and *d*. The undivided edges of *a b* and *c d* are shorter than the divided edges, but the undivided edge of *a b* is longer than the undivided edge of *c d*, and it is interesting to note that in the region corresponding to *b* of the edge *a b* a second pore appears,

much smaller than the one posterior to it and without any ducts opening into it. Apparently the greater length of this edge has afforded space, as it were, for the formation of another pore, but the ducts connecting with it fail to appear. This case, like a number of others, shows that the pore may be wholly unconnected with the other organs, but that its formation is doubtless due to the general conditions that lead to the formation of the other portions of the set, even though the two parts do not unite.

Figure 41.

This case is very similar to the one shown in Fig. 40. The development is so far advanced that it is impossible to determine with certainty whether the division of the ducts is as complete as in that case. The cell-masses at the right representing the two ovaries and vitellaria appear about equal in size, and there are indications that they were connected with the single duct leading to the pore. It is impossible to determine whether the vas deferens divides or not.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO,
May, 1900.

A CONTRIBUTION TO THE DEVELOPMENT OF PARYPHA CROCEA.[1]

CARRIE M. ALLEN.

My work has been carried on at the Zoölogical Laboratory of Syracuse University under the direction of Dr. C. W. Hargitt, to whom it is a pleasure to express my obligations for his kind suggestions and supervision throughout its progress, and for the pains which he has taken in furnishing me with the best of appliances and material. The material upon which the investigations have been made was collected by Dr. Hargitt at Woods Holl, Mass., during the summer of 1898. Through his kindness I had at my disposal an almost limitless supply killed and preserved by a number of methods. Picro-sulphuric acid and Perenyi's fluid both gave excellent results, but formalin proved unsatisfactory for histological work.

In most of my study I used preparations stained *in toto* in borax-carmine. The specimens were left in alcoholic borax-carmine for twelve hours, after which the stain was extracted by acid alcohol for from fifteen minutes to half an hour. In dehydrating they were left in each of the various grades of alcohol for thirty minutes, after which they were cleared either in cedar oil or chloroform. Both clearing agents gave good results, but the latter was preferable because of its rapid action.

In staining on the slide, iron-haematoxylin and double stain of eosin and haematoxylin both proved satisfactory.

In using the iron-haematoxylin the sections were fixed to the slide, carried down through the alcohols to 50 per cent, and placed in a 2 per cent solution of ammonio-ferric-alum for from thirty minutes to three hours. They were then washed in running water for twenty minutes, stained in 0.5 per cent aqueous solution of haematoxylin for from one-half hour to

[1] *Contributions from the Zoölogical Laboratory*, Syracuse University.

two hours, washed again in running water and cleared for a few seconds in iron-alum. After rinsing in distilled water they were plunged into 95 per cent alcohol, carried up and mounted in balsam. The best results were obtained by leaving the slides in each stain for an hour. This method was of greatest value in study of the segmentation of the egg. The cytoplasm appeared gray, chromatin fibers black.

In using the eosin-haematoxylin method the sections were stained for an hour in a 2 per cent solution of eosin in 90 per cent of alcohol, after which they were stained in a weak solution of Delafield's haematoxylin for twenty minutes. This stain gave very good general differentiation, and was of especial value in determining the origin of the sex cells.

A number of other stains and combinations of stains were used with fair success.

General Description of Parypha.

Parypha crocea is found all along the New England coast attached to floating timbers and the piles of wharves. It seems to prefer brackish water and partial sunlight, but often occurs in pure sea water.

This hydroid grows in colonies which arise from a single individual by a process of budding, and the sexes are always separate. The hydrorhiza is made up of a contorted mass of irregularly branched stems, from which the hydrocaulus of the individual hydroid arises. The stems bearing the adult polyps are usually two and a half to three inches in length, and short stems are sometimes found branching out from the main ones. Enclosing the stem is a horny, often annulated sheath, the perisarc. The polyp is borne at the top of a somewhat globular expansion of the hydrocaulus, and is almost conical in form, with a broad, saucer-shaped base. It contracts about three-quarters of the way up, forming a thick-walled, flexible proboscis, in the center of which lies the mouth, surrounded by a circle of short, thick tentacles with decurrent bases. Around the base of the polyp is a circle of long, slender tentacles, varying in number from sixteen to twenty-four. The medusoids

are borne upon long, slender, branched peduncles which arise a short distance above the tentacles of the lower row. All parts of the hydroid are made up of the two layers characteristic of all hydroids, but the mesogloea forms only a thin layer in the peduncles and tentacles and is not visible in the medusoids. The tentacles of both rows consist of a central axis of the endoderm, surrounded by a thin layer of ectoderm.

Origin and Morphology of Male Gonophores.

The medusoids in this species begin to appear early in the development of the hydroid, when the head upon which they are borne is less than a quarter of the size of the adult polyp. The first indication of their formation is a slight outpushing of the endoderm of the body wall a little above the axils of the lower row of tentacles. The ectoderm is pushed out and becomes thinner than in the adjacent parts of the wall. The papilla thus formed elongates into a peduncle communicating directly with the body-cavity of the polyp. From this peduncle arise short branches which may subdivide, and it is at the ends of these that the medusoids are borne. At first there is merely a thickened layer of endoderm surrounded by a thin layer of ectoderm, but when the length of the bud is about once and a half the width, the ectoderm cells at the tip begin to grow rapidly, forming a plug of cells with large nuclei and indistinct boundaries (Pl. I, Fig. 1). For a time the endoderm is forced back (Pl. I, Fig. 2), but it soon begins to grow down into the center of the plug, to form the manubrium, and around the outside to form the endodermal layer of the bell. All the cells between this layer and the manubrium are of ectodermal origin, and from them the reproductive elements arise. The sex cells increase in number, and to some extent in size, until they occupy the greater part of the bell. While this growth is taking place the cells at the distal end of the gonophore next the endodermal layer of the bell begin to differentiate, forming a thin, delicate layer which gradually extends around the gonophore and becomes the inner wall of the bell (Pl. I, Fig. 3). It is made up of cells much smaller than those from which they

are derived. Meanwhile the endodermal layer has thickened in four regions equidistant from each other at the distal end of the medusoid. At first the cells in the thickened region are irregularly arranged, but later they form themselves into two rows with a space between them. In a few cases no cavity was found, and in two of the gonophores examined it extended halfway around the bell. The remainder of the wall consisted of a single layer. Pl. I, Fig. 4, represents the condition found in most of the medusoids. Agassiz ('62), p. 259, states that there are neither radial nor circumoral canals in this species but the position and mode of development of these cavities leave little doubt that they are rudimentary radial canals. No circular canals were observed, and the radial canals were never found connected with the body cavity of the medusoid in any of the hundreds of sections studied.

Spermatogenesis.

The large nucleated cells lying between the manubrium and the inner wall of the bell become the sperm mother-cells, which finally break up to form the sperms. In the first division the karyokinetic figures are distinct and show spindles and prominent chromosomes. The later stages were difficult to study because of the minuteness of parts, and I was unable to demonstrate clearly the exact number of spermatozoa derived from a single germ cell, but I think four are usually formed. Their structure could only be made out in particularly favorable sections, but was easily demonstrated by crushing the gonophore and allowing the sperms to escape. They consist of a pear-shaped head with a very long, slender tailpiece. When fully developed the male gonophores are spherical, and the walls are so thin that their structure can only be determined by the use of very high powers. They bear no tentacles, although the ectoderm is sometimes thickened slightly in the regions where tentacles arise in the female. I examined carefully a large number of mature male gonophores to learn whether or not the ectodermal layer of the manubrium was formed and discovered a definite transparent layer next the

endoderm. No gonophores from which the sperms had been expelled were found, so I was unable to prove that this represented the ectoderm of the manubrium, but as that layer was not observed in the female until a very late stage, I think that there can be little doubt that it functions as such.

Origin and Morphology of the Female Gonophore.

The female gonophores arise in the same manner as the male and, in the early stages, are made up of the same parts, but later may always be distinguished by a circle of six or eight short, blunt tentacles at the distal end and by their more elongated shape. When filled with young they are nearly spherical and the tentacles mere papillae; but when the larvae have been set free the medusoids become elongate and the tentacles expand. Pl. I, Fig. 5, shows a section through two of these tentacles.

Oögenesis.

The primitive egg cells are developed in the same manner as the sperm mother-cells. I find no evidence whatever of ova either in the coenosarc of the stem, the body of the polyp, or the walls of the peduncle. There are in the endoderm of the polyp and peduncle numerous large, deeply stained cells with large nuclei which somewhat resemble eggs when cut in the right plane, but a careful study of a large number of sections reveals the fact that they are in reality highly differentiated endodermal cells. They are always in contact with the supporting layer and usually project beyond the other endoderm cells into the body cavity, neither of which conditions, according to Weismann ('83), p. 70, occurs in egg cells. Moreover, these cells are much larger than the primitive ova and take a deeper stain than do the eggs in any stage of their development. They are very rich in protoplasm, and sometimes the outer surface is found sloughing off into the body cavity. This condition was even more marked in similar cells in Eudendrium ramosum, where they extend farther into the body cavity, and the discharge of portions of their protoplasm was

very evident. All this would indicate that they were glandular in function. They are largest and most numerous in the peduncle and occasionally one is found in the manubrium, but such cases are rare. It would be impossible to distinguish a section through the peduncle of a male head from that of a female, as these cells are equally conspicuous in both. Pl. I, Fig. 8, shows a number of these glands, one of which resembles an egg, but other sections through the same peduncle show that it is really in contact with the supporting lamella.

In the younger stages of development the manubrium of the female appears to consist entirely of endoderm, but when the gonophore is fully mature and the primitive ova have disappeared, a thin layer of ectoderm is found to be present. It consists of a single layer of much flattened cells with smaller nuclei than those of the germ-tissue cells from which they are derived.

Development of the Ovum.

The primitive egg cells make up the large mass of tissue lying between the manubrium and the inner wall of the bell. They are packed closely together, so that the outlines of the cells are more or less irregular. The nuclei are large and spherical and contain a prominent nucleolus which takes a very deep stain. The mass of protoplasm surrounding each nucleus is small, and the cell boundaries are very indistinct (Pl. I, Fig. 4).

As the gonophore grows older the nuclei of the germinal tissue become much larger and more prominent, the mass of protoplasm surrounding them increases in bulk, and the cell boundaries become more clearly defined. At this stage the nuclei appear as very large spheres, with the chromatin fibers arranged in a sort of network around the periphery. Within the layer of chromatin is a colorless mass, near the center of which lies the nucleus suspended by four or five slender threads, which run out to the layer of chromatin. These threads take a fainter stain than the chromatin fibers and are only visible in especially well prepared specimens.

The nucleolus is usually spherical or slightly elongated,

but in many cases it shows a varying number of short, blunt processes. This condition was most clearly seen in sections stained with ammonio-ferric-alum and haematoxylin.

Within the nucleolus are a number of small, transparent, highly refractile bodies, the nature of which will be discussed later. There is usually one of these in the nucleus of each primitive ovum, but some contain two. As the ova grow older the number increases and there are sometimes as many as four or five in a single nucleolus. The protoplasm of the cells is granular and often contains a few small vacuoles.

Up to this time the growth of the various cells of the germinal tissue has been about equal, but now several cells increase markedly in size, and often the greater number in one side of the gonophore are found to be thus growing. If, however, a large number take part in this early development, the cells in the opposite side of the gonophore decrease in size, both nucleus and cytoplasm becoming smaller. Soon a few cells attain greater size than the rest and develop very rapidly. Many of the cells in this and the preceding stages are found to possess pseudopodia-like processes quite similar to those figured by Doflein ('96) for Tubularia. Smallwood ('99) mentions the same condition in the eggs of Pennaria. The pseudopodia extend in between the other primitive egg cells, and the tips are more granular and take a deeper stain than the rest of the egg. Doflein ('96) has given much attention to the amoeboid forms assumed by eggs of Tubularia, and he inclines to the belief that these processes do not function as mouths by which the surrounding eggs are bodily engulfed. My results have coincided very closely, in most respects, with those of Doflein, but numerous cases were also observed where the outline of the absorbed egg could be definitely made out within the protoplasm of the absorbing egg. Even in these cases, however, the absorbed egg did not lie in a vacuole, as would the food taken in by the amoeba, and the outline could only be made out by the greater density of its protoplasm. It seems, therefore, that in this case also we have a blending of the protoplasm of the two cells rather than a digestion and absorption of the one by the other. There seems to be no great uniformity either

in the number or location of the primitive cells which finally become ova, although by far the greater number lie next the manubrium, and few, if any, develop on the outer surface of the germinal mass. I am inclined to agree with Doflein ('96), p. 65, that all of the cells of the germinal tissue have potentially the capacity of becoming eggs, but that those favored by better nourishment or advantage of position are the first to develop.

He says in this connection : " Das starke Wachsthum des Gonophors hat einzelne Lücken und Spalten im Gewebe entstehen lassen, und in diese wachsen nun die Keimgewebezellen mit ihren Fortsätzen hinein." But while in my investigations many such cracks were found, in most instances the pseudopodia extended between eggs where no crack occurred, and in the greater number of ova no pseudopodia were present at all. I am, therefore, led to the belief that proximity to cracks in the germinal tissue is not of controlling importance, although the eggs do undoubtedly take advantage of the room afforded by such cracks when present. Doflein ('96) also states that in Tubularia the growing eggs are always found next the manubrium or upon the outside of the germinal mass, unless cracks are present within the tissue. I have examined a large number of sections, and I find that in Parypha the eggs of the outer layer are the last to develop, but that those in the interior of the germinal tissue are often found considerably enlarged even in the younger gonophores.

When the growing cells have attained a diameter about three or four times that of the cells of the germinal tissue, the nucleus is found lying close to the periphery of the egg and is oval and transparent, the chromatin fibers being scarcely visible (Pl. II, Figs. 5, 6). The nucleolus takes a fainter stain, and in most cases contains a number of the refractile bodies already mentioned. Later these bodies apparently unite, as nearly the whole nucleus is often occupied by a single large one. Just what their character is I am unable to state, but they appear to contain oil, and certainly they are associated with the peculiar metabolism exhibited by the cell at this time (Pl. II, Figs. 5–7). In some of the eggs in which the nucleus had this peripheral position, its outline was irregular upon the

inner side so that it resembled the figure shown by Hickson ('90) to illustrate the stage in the fragmentation of the oösperm nucleus of Allopora. In the next stage the nuclear membrane is broken down and the nucleoplasm blends with the cytoplasm of the egg, from which it can only be distinguished by its homogeneousness and greater transparence (Pl. II, Figs. 7, 8). In other eggs having the same general appearance as the last no nucleus whatever is visible. I have several complete series through eggs in this stage, none of which show any signs of a nucleus, although they have been stained by a number of different processes, and I am perfectly confident that the nucleus would be visible if present. Hickson describes a similar condition in the eggs of Allopora, Milleopora, and Distichopora; and Dr. C. W. Hargitt tells me that in his opinion a like condition is to be found in Eudendrium, although he has not yet placed it beyond doubt.

Hickson ('93) has written an extended account of "nuclear fragmentation," in which he cites the opinion of a number of authors with regard to this much disputed question. After describing the stages observed in Distichopora he says: "I have described a process which can only be compared with the so-called free nuclear formation in the early insect embryos. Nuclei make their appearance in places which were previously devoid of any nucleus or nuclear structure. It is not reasonable, however, to assume on the insufficient evidence before us that "nuclear formation" does actually occur. It seems to me much more probable that minute fragments of nuclear substance scattered through the protoplasmic meshwork collect together in places, and form by their fusion true recognizable nuclei. In other words, the process we have under observation is rather one of "nuclear regeneration" than one of free "nuclear formation." He quotes Flemming and Ziegler as authorities most opposed to this view, both these investigators contending that any process of nuclear division other than that by mitosis is a sign of the degeneration of the nucleus and the approaching end of the life of the cell. Ziegler inclines to the opinion that nuclei which have arisen by amitotic division will never again divide mitotically. Opposed to these are the works

of Verson, Frenzel, Löwit, and others who, since the publication of Ziegler's paper, have called attention to cases of amitotic division of the nucleus which are certainly not followed either by nuclear degeneration or a cessation of cell multiplication. Altogether there seems to be constantly increasing evidence that such a fragmentation does occur in the ova of widely separate groups of animals.

Wilson ('96), p. 85, believes that the subject requires more study, but says: "There can be no doubt, however, that Flemming's hypothesis in a general way represents the truth, and that in the majority of cases amitosis is a secondary process which does not fall in the generative series of cell division."

Absorption.

At about the time when the transparent nucleus lies near the periphery of the egg the cytoplasm changes from a granular to a reticular structure. The boundaries between the large cells and those adjacent to them now begin to break down and the protoplasm to blend. This fusion may take place between two large cells or between a growing cell and a germ tissue cell. The former usually occurs first, the large cells near the manubrium fusing and then gradually taking in the germ cells which surround them. The nuclei of the latter are found lying in the protoplasm of the absorbing cell. Both conditions are shown in Pl. I, Figs. 6, 7.

The outline of the syncytium thus formed is very irregular, and parts of the walls of the constituent cells persist for a time, showing where the fusion has occurred (Fig. 7). Doflein ('96), p. 66, states that in Tubularia one large, well-nourished cell controls the absorption, and that as it grows its nucleus also increases in volume, and that the nucleus becomes the functional nucleus of the ovum, the other nuclei being gradually absorbed. In Parypha, as already stated, the nuclei of the growing cells disappear at an early stage so that only the nuclei of the smaller cells persist. It thus becomes impossible to tell which is the controlling cell.

Finally the mass of fused cells takes on the typical egg

form, the protoplasm near the periphery becomes more dense, and the absorbed nuclei are found in various stages of disintegration. The egg now lies on the outside of the mass of germinal tissue and next to the wall of the bell. No evidence of fusion with the primitive eggs was observed after this stage was reached, although the two were still in contact. It is quite evident, however, that the remaining germ cells grow and unite to form new eggs later in the history of the parent, since primitive eggs are often found in advanced stages of growth, while two or three nearly mature embryos still occupy the gonophore. In other cases the gonophores contained several embryos in various stages of development, but no primitive ova. Doflein ('96), p. 67, states that, although he was unable to obtain sections to illustrate adequately the point, he believes that the germ cells of Tubularia do unite to form new eggs after the larvae have left the gonophore. In Parypha there is no chance to doubt that new ova are formed even before the exit of the larvae.

Fertilization.

As is the case in many of the hydroids, the process of fertilization is shrouded in mystery. The fact that the eggs are developed in closed gonophores makes it difficult to decide just when fertilization takes place. In discussing the development of Allopora, Hickson states that he believes that fertilization occurs while the nucleus lies at the periphery of the egg, and previous to the time when it becomes irregular in outline. From the positions of the eggs in which these irregular nuclei were found, *i.e.*, next the manubrium, this might be the case here, but nothing was discovered which threw any light directly upon the matter.

History of the Pseudo-Cells.

The nuclei of the absorbed cells are found in various stages of disintegration within the ovum. Some of them resemble so closely the nuclei of the germ-tissue cells that, were it not for the position and the vacuoles within which they lie, it would be

impossible to distinguish them. Later the chromatin fibers lose their reticular arrangement and assemble into a varying number of small spheres just within the periphery of the nucleus, and at the same time the threads which support the nucleolus disappear. The ground material in which the chromatin is suspended, and which up to this time has been nearly transparent, now begins to react to the staining agents, and the structure of the nuclei becomes obscure. If, however, methyl-blue was used, this substance was only slightly affected, so that this stain proved most satisfactory for the study of the various phases exhibited by the retrograding nuclei, or pseudo-cells, as they are sometimes called. Many of the nuclei are often found in the process of division. The nucleolus lengthens slightly, and finally separates into two parts. Later the entire nucleus divides and part of the chromatin goes with each half. Cases in which the nucleolus had divided were very numerous, but very few were found in which the division was actually taking place. Pl. II, Fig. 11, shows such a one, and Fig. 10 represents a nucleus in which there were three processes on the nucleolus. No chromatin fibers were visible in either of these cases. The halves thus formed often divided again, sometimes before they were separated, and in some instances as many as six parts can be observed. The chromatin globules vary in number and size in the various parts (Fig. 12). In some of the nuclei the division is less regular, and portions are often found in the process of being absorbed into the protoplasm of the egg. Fig. 15 represents a nucleus in which the parts formed by the first division were of very unequal size. In the smaller the nucleolus has again divided, but the larger part has been partially absorbed. Often several of these nuclei are found in a single vacuole. Fig. 9 shows one in which there were seven in various stages of disintegration, but usually not so many are found. Doflein believes that they are carried into the vacuoles by currents in the protoplasm. All this goes to strengthen the opinion of Doflein that the absorbed nuclei take the place of the yolk-granules, which are wanting in this species, and that they are gradually broken down to serve as food for the developing egg. They persist through the entire

embryological development, being very numerous in the endoderm of the young hydroid when it escapes from the gonophore. Isolated ones are even found in the endoderm of the tentacles, as noted by Doflein, but I cannot agree with him that they are entirely confined to that layer.

Segmentation of the Ovum.

The egg, after assuming the typical form already described, goes into a resting stage, as a large number are found in that condition and without nuclei. Soon, however, an irregular mass of nuclear matter appears at one pole. Sometimes this forms a single mass, in other cases it is made up of two or three more or less isolated portions. Whether these are finally assembled to form a single nucleus, or whether two or three nuclei are thus produced, I am unable to say, as many of the sections in the later stages might be interpreted either way. In some of the eggs a single definite star-shaped nucleus was present, but in others there were two, and in one case four of these nuclei lying close together at one pole of the egg. There was nothing in these eggs to indicate that the nuclei had not been derived from a single nucleus, but, on the other hand, some of the disorganized masses of nucleoplasm could not but give the impression that more than one would be formed. However, the number is of minor importance, and the real interest attaches to the fact that such a reorganization occurs at all. That it does, I am fully convinced. I have examined a large number of sections with this question particularly in my mind, and am forced to the conclusion that the nucleus of the mature egg is formed by the reorganization of the fragments of the nuclear matter scattered through the cytoplasm.

The earliest stage in which definite mitosis was observed was in the egg shown in Pl. III, Fig. 1. In this three definite nuclei, one in a process of division, showed in a single section. Another section through the same egg revealed a fourth nucleus which, from its position, might have been derived from one of the others, but no spindles were observed. There were no signs whatever of segmentation planes in this egg. The development in the eggs of Parypha is very irregular indeed,

and seems to be governed by no single law. In some cases definite cell walls were found in the earlier stages, as in Fig. 2, where four cells had been formed, one of which contained two nuclei. In this we have only the stage next to the one last described, but in that there were no segmentation planes at all. In still later stages the development is quite as irregular. Fig. 5 shows a section in which six nuclei were visible, and other sections through the same egg contained several others, some of which were in the process of division, but no cell walls had been formed In Figs. 6 and 7 we have sections through much older eggs, but the same indefiniteness of structure prevails. From the foregoing illustrations it will be seen at once that there is little uniformity in the early development of the eggs of Parypha, either as to size of the cells formed or the number of nuclei that appear previous to the formation of the cell walls. Segmentation does, however, begin at one pole, and the greater part of the egg is for a time unsegmented. In no case did I find the egg divided into two equal parts, as Dr. Hargitt has sometimes observed in Pennaria eggs. Pl. III, Fig. 3, represents conditions similar to what is constantly met with in eggs of Pennaria. In total segmentation the ovum consists of a solid sphere of cells of more or less uniform size but with irregular outlines. They are very reticular in structure, and large vacuoles are numerous.

Formation of the Ectoderm.

Following the complete segmentation, the first indication of a differentiation into ectoderm was observed in an increased amount of cytoplasm in the outer layer of cells. These cells then divide radially, forming narrow cells, as shown in text Fig. 1. The two mitotic figures lay in adjacent cells, as shown in the drawing. In the next stage observed the ectoderm appeared to consist of two layers of cells much smaller than those of the endoderm, and distinguished from them by the greater density of protoplasm. The two layers appeared in this case to be dovetailed into each other, as shown in Fig. 2 of the text. In the fully formed ectoderm the cells are very elongate and somewhat

spindle-shaped, with one end broader than the other. Both the form of the cells and the position of the nuclei indicate that they have been formed from a condition like that in Fig. 2, and not by further delamination of the outside layer alone. At this stage the larva is made up of a solid mass of irregular cells with spherical nuclei surrounded by a single layer of much elongated cells. No segmentation cavity is formed. The origin of the germinal layers agrees, therefore, quite closely with that described by Hickson ('93) under *E. e.*, p. 52: "A sterrula is formed by precocious delamination. No segmentation cavity is formed, and segmentation is at first incomplete." Parypha is not mentioned by Hickson under this class, and Tubularia, the form most like Parypha in its general mode of development, he includes under another head. Dr. Hargitt informs me that nothing equivalent to true delamination or invagination occurs in Pennaria. It would, therefore, seem that no one, two, or even three laws of cleavage are sufficient to explain the varied conditions to be found in the segmentation of the hydroid egg.

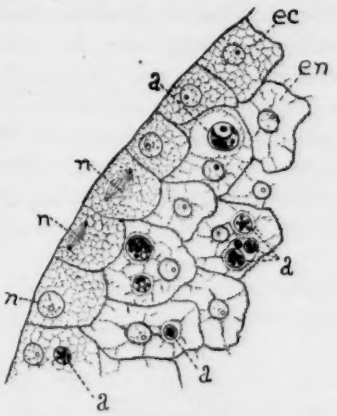

FIG. 1 × 560. — Early stage in the formation of the ectoderm of the embryo; *ec*, ectoderm; *en*, endoderm; *n*, nuclei; n^1, nuclei in the process of division.

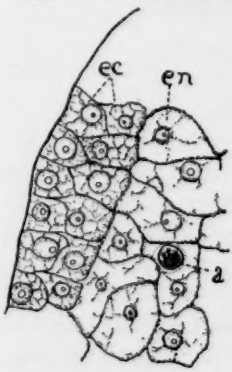

FIG. 2 × 560. — Later stage in the formation of the ectoderm; *ec*, ectoderm; *en*, endoderm; *a*, nuclei of absorbed cells.

The embryo now appears concave upon the side next the manubrium, but this is probably due to pressure and not to any intrinsic cause. After the formation of the ectoderm the two layers of the embryo evaginate at seven points so that a section through the region of the process appears star-shaped,

the rays at first being very short. These processes elongate to form the basal tentacles of the young hydroid. While this growth is taking place the convex side of the embryo becomes still more convex, and the concave portion between the tentacles evaginates and becomes convex also. In this way the endoderm cells in the center are split apart and the body cavity is formed. At first it is very irregular, but later the endoderm cells assume the typical endodermal form and arrange themselves in a single layer within the ectoderm, and the body cavity

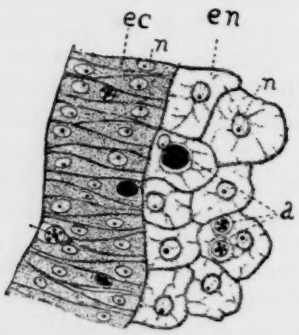

FIG. 3.

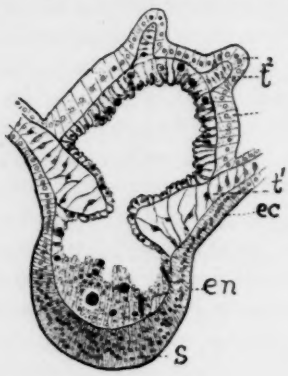

FIG. 4.

FIG. 3 × 560. — Fully formed ectoderm from convex side of embryo; *ec*, ectoderm; *en*, endoderm; *n*, nuclei; *a*, nuclei of absorbed eggs.

FIG. 4 × 190. — Young embryo ready to escape; t^1, basal tentacle; t^2, buccal tentacle; *s*, stalk; *ec*, ectoderm; *en*, endoderm.

takes on a form quite similar to that of a young polyp. From almost the earliest stage in the development of the ectoderm the cells on the convex side of the embryo appear much longer than upon the opposite side, and it is this portion which becomes the stem to which the young hydroid attaches itself. According to Agassiz the larva escapes in this condition, and the mouth and buccal tentacles are developed after it attaches itself. I have, however, obtained sections of a large number of mature larvae in which well-developed tentacles were present. Fig. 4 represents an embryo that was just leaving the gonophore. The body and the stem were both well developed, and the basal tentacles were nearly twice as long as the body.

At the buccal end there were five or six tentacles, a section of which is shown in the figure. Whether the mouth is developed at this time or later I did not decide.

Summary and Conclusion.

In a summary of the results obtained in this study, the following points should be noted:

1. The medusoid develops from a bud formed by an outgrowth of the body wall and shows itself first in a thickening of the endoderm.

2. The sex cells in both the male and the female are derived from the plug of ectodermal cells which is formed at the apex of the bud.

3. The medusoid is never set free and no circular canal is formed, although remnants of four radial canals are quite conspicuous.

4. The eggs grow by the absorption of the cells of the germinal tissue, a syncytium being thus formed.

5. The nuclei of the primitive eggs persist as pseudo-cells and are gradually broken down to serve as food for the growing embryos.

6. The pseudo-cells divide amitotically, but are finally absorbed by the growing egg.

7. The nucleus of the growing egg is absorbed at an early stage, but is re-formed, after the assumption of the typical egg form, from the fragments scattered through the protoplasm.

8. Segmentation is very irregular and nuclear division often outruns the segmentation of the egg.

9. The ectoderm is formed by radial delamination of the two outer layers of cells.

10. The embryo escapes as an actinula with both basal and buccal tentacles.

The results obtained in this investigation differ in several points from those of Agassiz, whose description of Parypha crocea is the only one that I have found. Clark ('93), to be sure, refers to the eggs and spermatozoa of this species, but gives no account of them. Agassiz states that he was unable to

find any trace of eggs, and that the embryos are developed from a large spherical portion which buds off from a granular mass of protoplasm formed by the separation of the endoderm and ectoderm in the medusoid bud. This granular mass he calls the "germ basis." A study of stained specimens in section shows clearly that this granular mass, or "germ basis," as he calls it, is really the mass of sex cells which have already been described. His opinion that the embryo was formed by the budding off of large portions of this mass probably arose from the fact that in the early stages of the development the eggs are packed closely together and the membranes are indistinct, so that the whole mass appears somewhat homogeneous. As the eggs grow, they become less granular and in time are entirely separated from the germ tissue. As to the radial canals, they would probably be overlooked, except in sections, as they are never functional. The tentacles of the embryo are, however, so well developed that it seems strange that he should not have observed them, since he has noted tentacles upon the female gonophore where they are less clearly defined.

SYRACUSE UNIVERSITY, May, 1900.

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EXPLANATION OF PLATE I.

FIGS. 1–7 × 190; FIG. 8 × 270.

FIG. 1. Young medusa bud showing the formation of the germinal cells from ectoderm of bud. *ec*, ectoderm; *en*, endoderm; *h*, germinal cells.

FIG. 2. Later stage, germinal cells separated from the ectoderm of the bud.

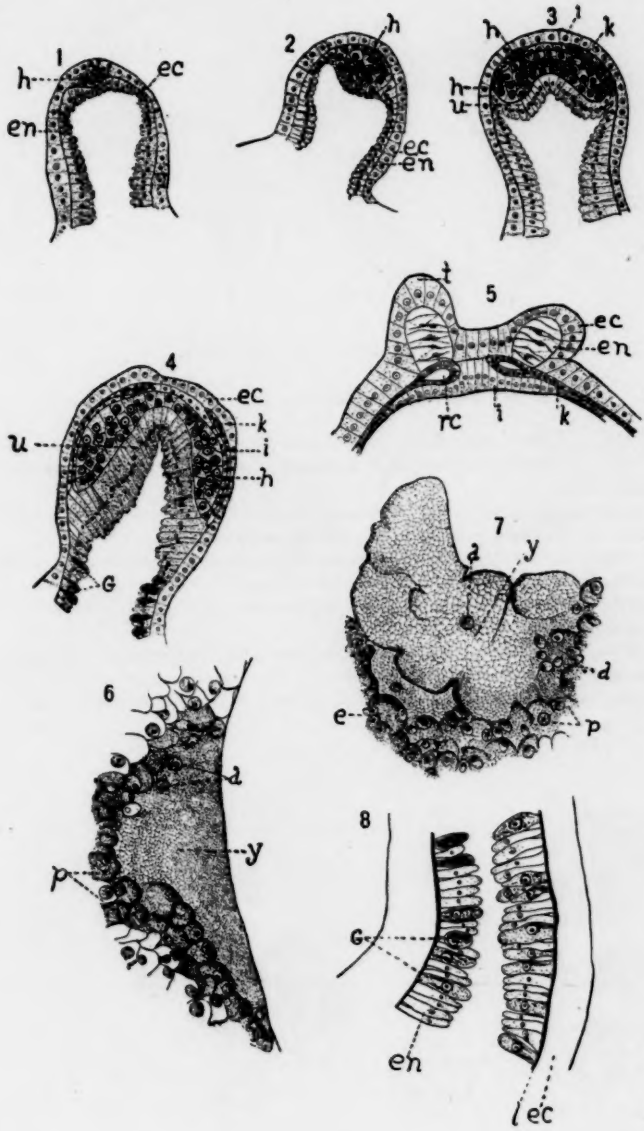
FIG. 3. Still later stage showing the mode of formation of the endodermal layer of the bell (*k*), the inner ectodermal layer (*i*), and the manubrium (*u*).

FIG. 4. Showing the layers of the bell completely formed.

FIG. 5. Distal end of mature female gonophore showing tentacles (*t*), rudimentary radial canals (*rc*), outer ectodermal layer of the bell (*ec*), and endodermal layer (*k*), inner ectodermal layer (*i*).

FIGS. 6, 7. Showing growth of the egg by the absorption of the primitive egg cells (*p*). Syncytium thus formed (*y*); nuclei of absorbed cells (*a*); young growing cell (*e*).

FIG. 8. Longitudinal section through peduncle from female head showing gland cells (*G*).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7
d
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p
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en
ec

EXPLANATION OF PLATE II.

FIG. 1 × 127; FIG. 2 × 118; FIGS. 3–8, 10–15 × 765; FIG. 9 × 495.

FIG. 1. Growth of ovum (*e*) by absorption of primitive cells (*f*).

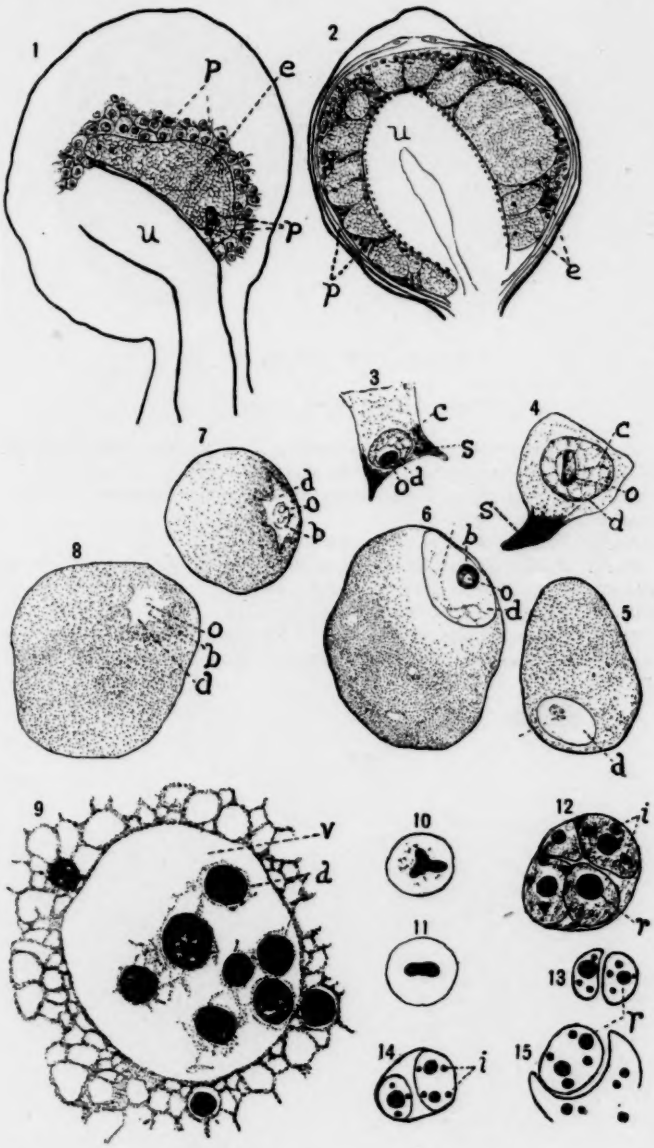
FIG. 2. Showing the number of growing primitive egg cells to be found in a single gonophore.

FIGS. 3, 4. Primitive egg cells in early stage of development showing pseudopodia (*s*); nucleus (*d*); oil drops (*o*); chromatin fibers (*c*).

FIGS. 5–8. Later stages showing the disappearance of the nucleus of the growing egg. *d*, nucleus; *b*, nucleolus; *o*, oil drops.

FIG. 9. Vacuole (*v*) in segmenting egg showing nuclei of absorbed cells (*a*) in various stages of disintegration.

FIGS. 10–15. Retrograding nuclei of absorbed cells. Nucleolus (*r*); assembled chromatin fibers (*s*). In Fig. 15 a portion of the nucleus has been absorbed; the smaller part is in the process of division, the nucleolus having already divided.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13
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i
15

EXPLANATION OF PLATE III.

FIGS. 2, 6 × 115; FIGS. 1, 3–5, 7 × 152.

FIG. 1. Young ovum showing three nuclei (*n*). n^1 in the process of division. No segmentation planes visible; *a*, nuclei of absorbed cells.

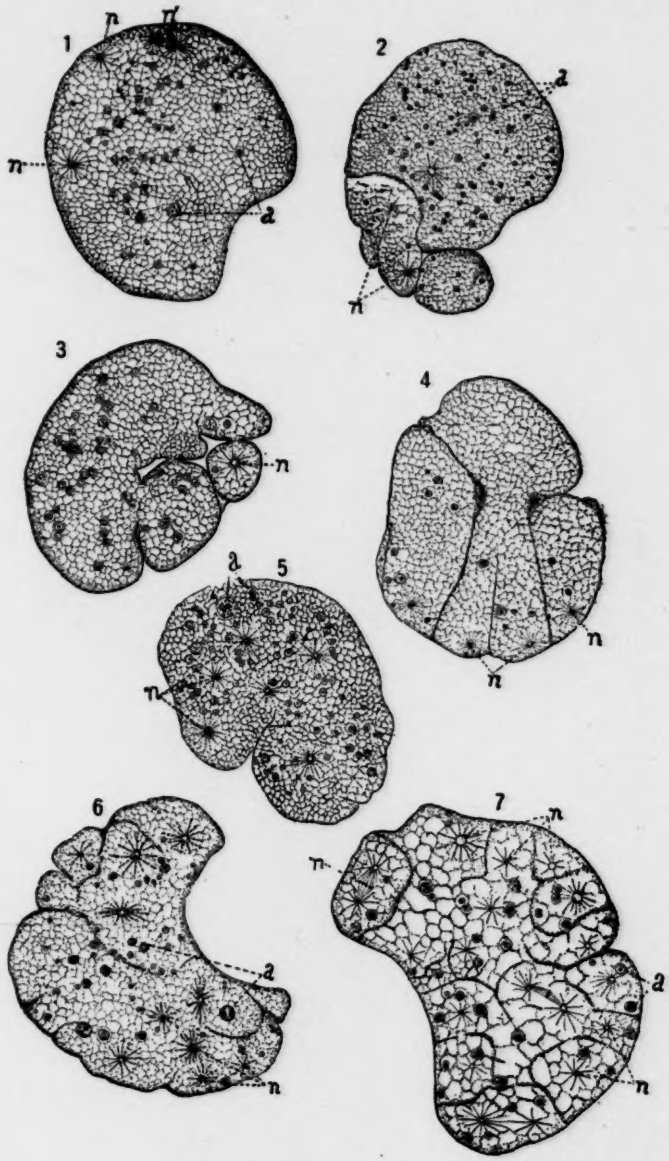
FIGS. 2, 3. Slightly later stages; segmentation planes well marked. *n*, nuclei; *a*, nuclei of absorbed cells.

FIG. 4. Still later stage of segmentation.

FIG. 5. Section through an egg containing fifteen or sixteen nuclei, but no well-defined cell walls. *n*, nuclei; *a*, nuclei of absorbed cells.

FIG. 6. Later stage; cell boundaries indefinite.

FIG. 7. Advanced stage of segmentation; cells irregular in outline, cytoplasm very reticular; *n*, nucleus; n^1, nuclei in process of division; *a*, nuclei of absorbed cells.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